# Rapidly shifting elevational distributions of passerine species parallel vegetation change in the subarctic

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**Abstract.** Despite predictions of poleward and upslope shifts in the distribution of breeding passerines under climate change, studies often report variable responses with some species shifting opposite of the expected direction and others showing range stability. While changes in climate could affect distribution directly, passerines show strong preferences for particular structural vegetation characteristics, suggesting that long-term changes in vegetation may mediate a species' distributional response to climate, and consequently, may be responsible for the observed heterogeneity. We assessed changes in the elevational distribution and occupancy probability of 17 passerine species in Denali National Park, Alaska, from 1995 to 2013 across an elevational gradient containing multiple topographically defined ecotones (treeline and shrubline). An upward distributional shift was pervasive among shrub-tundra species, corresponding with observed expansion of shrub cover at higher elevations. Forest-associated passerines showed a weaker response as a group with some species showing range stability or retraction, while others exhibited modest expansions that were consistent with an advancing treeline ecotone. Denali's mean summer temperature increased significantly over the past century, but remained relatively stable over our study period, implying that longer term changes in climate indirectly influenced bird distribution through changes in woody vegetation. Further, heterogeneity in the response of forest-associated species was consistent with a slower rate of forest development and expansion as compared with shrub colonization. Together, our results indicate that the elevational range dynamics of passerines may be related to species-specific associations with different vegetation communities and variation across these vegetation communities in the timescale over which distributional change is occurring.

**Key words:** climate change; long-term monitoring; passerines; shrub expansion; treeline.

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## INTRODUCTION

Global climate change is expected to have dramatic effects on species' distributions and abundance patterns across taxa (Root et al. 2003). In particular, the Arctic is warming at two to three times the global rate (Overpeck et al. 1997, ACIA 2004, Trenberth et al. 2007). Across interior and northern Alaska, landscape-scale changes have been observed including permafrost degradation (Jorgenson et al. 2001, Osterkamp et al. 2009), increases in wildfire frequency and intensity (Kasischke and Turetsky 2006, Beck et al. 2011), wetland shrinkage (Riordan et al. 2006, Roach et al. 2011), and changes in vegetation distribution and structure (Chapin et al. 2005,

Tape et al. 2006). One of the most visible changes related to a warming climate in Alaska is the rapid expansion of woody vegetation (e.g., erect shrubs) across open landscapes (Sturm et al. 2001, 2005, Tape et al. 2006) and into higher elevations (Stueve et al. 2011). In Denali National Park and Preserve (Denali) in interior Alaska, trees (*Picea glauca* and/or *Populus balsamifera*) are becoming established in formerly treeless areas, including higher elevations, and erect shrubs are expanding by invading open wetlands and colonizing formerly open floodplains and terraces (Roland and Stehn 2014). Empirical studies of range dynamics in the Arctic and subarctic have been primarily restricted to vegetation patterns (e.g., Tape et al. 2006, Stueve et al. 2011); however, changes in the spatial distribution of vegetation affect the distribution and/or abundance of terrestrial vertebrates including passerine birds (Henden et al. 2013).

Changes in the distributions of birds are often used to address hypotheses about directional shifts in distribution due to climate change. These studies predominantly report a pattern of poleward or upslope movement in response to climate warming (Hitch and Leberg 2007, Maggini et al. 2011, Tingley et al. 2012). However, they also indicate variable responses, with many species exhibiting downslope shifts or no detectable changes despite clear changes in broad-scale climate factors (Parmesan and Yohe 2003, Archaux 2004, Popy et al. 2010). Heterogeneity in the response may reflect variation in the lag time and temporal scale of species' responses (Chen et al. 2011). Ultimately, unexpected patterns may arise through differences in life history and physiological traits of species (Moritz et al. 2008, Pöyry et al. 2009, Tingley et al. 2009, 2012), the interaction of various abiotic and biotic factors (Hutchinson 1957, Davis et al. 1998, Araújo et al. 2005, Chen et al. 2011), or as a direct response to abiotic factors including temperature and precipitation (Tingley et al. 2009, 2012).

The simplicity of species-climate distribution models, which assume that patterns of distributional change are the result of species tracking their climate envelopes over geographic dimensions, is appealing because it suggests that predicting distributions under climate change is relatively straightforward (Davis et al. 1998, Beale et al.

2008). However, interacting biotic factors (e.g., habitat, interspecific competition, and source-sink dynamics) mediate a species' distributional response to climate, and consequently, may be responsible for observed heterogeneity (Hutchinson 1957, Davis et al. 1998). Nevertheless, the linkage between distributional change and abiotic factors alone has received significantly greater consideration than the role of biotic factors in explaining observed patterns. As a whole, these studies have found varied levels of importance for species-climatic associations in explaining distributional patterns. For example, Beale et al. (2008) found that climate envelope models were poor predictors of distribution for the majority of European bird species that they considered. In an analysis of Swedish Breeding Bird Survey data, Tayleur et al. (2015) found that only 20% of species showed directional changes in distribution that tracked changes in temperature. In contrast, Tingley et al. (2009) documented climatic niche tracking among birds breeding in the Sierra Nevada Mountains of California using historic (1911–1929) and modern (2003–2008) survey data. Among the 53 species that they considered, 48 shifted their distributions to track changes in the distribution of temperature and precipitation. However, their analysis was structured to compare site occupancy at two points in time (i.e., observations were grouped into historic and modern periods) restricting inference to whether the long-term trend in climate was correlated with directional changes in bird distribution. In some cases, weather events directly influence bird distribution and population dynamics. However, climatic factors may also indirectly affect bird distribution through changes in vegetation. Passerine species select breeding and foraging sites in particular habitat types and structures and, by virtue of their high mobility, have the capacity for rapidly adapting to changes in vegetation by modifying their breeding distributions (Hitch and Leberg 2007).

Some types of ecotones are assumed to be well-suited for detecting distributional responses to climate change due to their sensitivity to changes in temperature and the distinctive nature of vegetation structure near their margins (Risser 1995, Kupfer and Cairns 1996, Loehle 2000). The sensitivity of ecotones to climate change is thought to be heightened in montane environments where variation in climatic factors is compressed along steep

elevational gradients (Beckage et al. 2008). Measurable upward migration of treeline in the subarctic, in the absence of a large-scale disturbance such as fire, occurs over decadal scales and longer due to the slow rate of tree recruitment and the low frequency of viable seed production at treeline (Zasada et al. 1992, Kupfer and Cairns 1996, Roland et al. 2014). In contrast, shrub colonization of open habitats, infilling, and increases in canopy height are relatively rapid in tundra environments (Tape et al. 2006, Myers-Smith et al. 2011, Roland and Stehn 2014). Therefore, passerine species breeding in shrub-tundra might be expected to show more rapid distributional and population-level responses than those species associated with upland forest and/or the treeline ecotone. Further, high-elevation species with elevational distributions centered near shrubline might be expected to exhibit the largest distributional responses due to their more compressed elevational ranges and the sensitivity of their range margins to relatively rapid structural change. Temporal changes in species distributions corresponding to these predicted relationships would provide context for observed heterogeneity in responses to climate warming. Such changes may also help identify those species most at risk from continued climate warming in the subarctic.

We used repeated point-count data collected between 1995 and 2013 in Denali to assess changes in the elevational distribution and occupancy probability of 17 passerine species across an elevational gradient traversing both treeline and shrubline ecotones in Denali. Using an occupancy modeling approach, we assessed temporal trends in occupancy and elevational distribution for each passerine species. We predicted the largest changes in occupancy and distribution for those species with distributions centered near shrubline because the distribution of shrubs changes more quickly than that of mature forest, absent large-scale disturbance. Similarly, we predicted weaker and more variable responses among forest-associated species with those species associated with mature forest least likely to show distributional responses due to the relatively slow rate of treeline advance and mature forest establishment. Our specific objectives were to 1) assess temporal trends in species elevational distributions and occupancy rates; 2) relate distributional responses to species-specific habitat associations to help explain the pattern of

responses; and 3) identify species or assemblages most at risk under continued climate warming.

## METHODS

### Study area

We conducted passerine surveys along the easternmost 118 km of the 144 km Denali Park Road (DPR) in the northeastern portion of Denali (63 °35.8′ N, 149 °38.2′ W) (Fig. 1). The DPR, narrow and unpaved for all but the eastern 24 km, winds through the northern foothills of the Alaska Range crossing mountain passes, riparian zones, and extensive upland areas. It traverses upland coniferous forest, sparsely canopied woodland at treeline, dense riparian and upland shrublands, open shrublands near shrubline, and open alpine habitats including tundra and fellfield. Treeline is characterized by open *Picea glauca* woodlands with *Betula* and *Salix* spp. shrub understory in uplands and by stands of *Populus balsamifera* and *P. glauca* in floodplain and terrace environments. The position of treeline is variable depending on exposure, but occurs between approximately 850–1100 m. Shrubline is characterized by a low, open birch-ericaceous-willow vegetation mosaic (depending on topography) grading into *Dryas* and/or mixed dwarf shrub tundra or open barren slopes in steeper or particularly exposed sites. Shrubline varies depending on site factors, but shrub cover diminishes substantially above 1100 m, and shrubs >50 cm in height are a minor component of the vegetation above 1200 m (C. Roland, unpublished data).

### Data collection

We established three roadside survey routes each comprising 50 points with 0.8 km spacing. Trained observers conducted repeated surveys from late-April to early-July during 10 yr (1995–1998, 2006, and 2009–2013), and routes were surveyed 2–18 times in each year (mean = 6.3 visits/year). Standard 3-min point-count surveys were conducted during favorable weather from 0.5 h before sunrise to approximately 6 h thereafter (Bystrack 1981). All birds seen or heard within ~400 m during the count period were recorded (Bystrack 1981), but only detections of singing males were used for our analyses. The same routes were generally surveyed by multiple observers in each year and
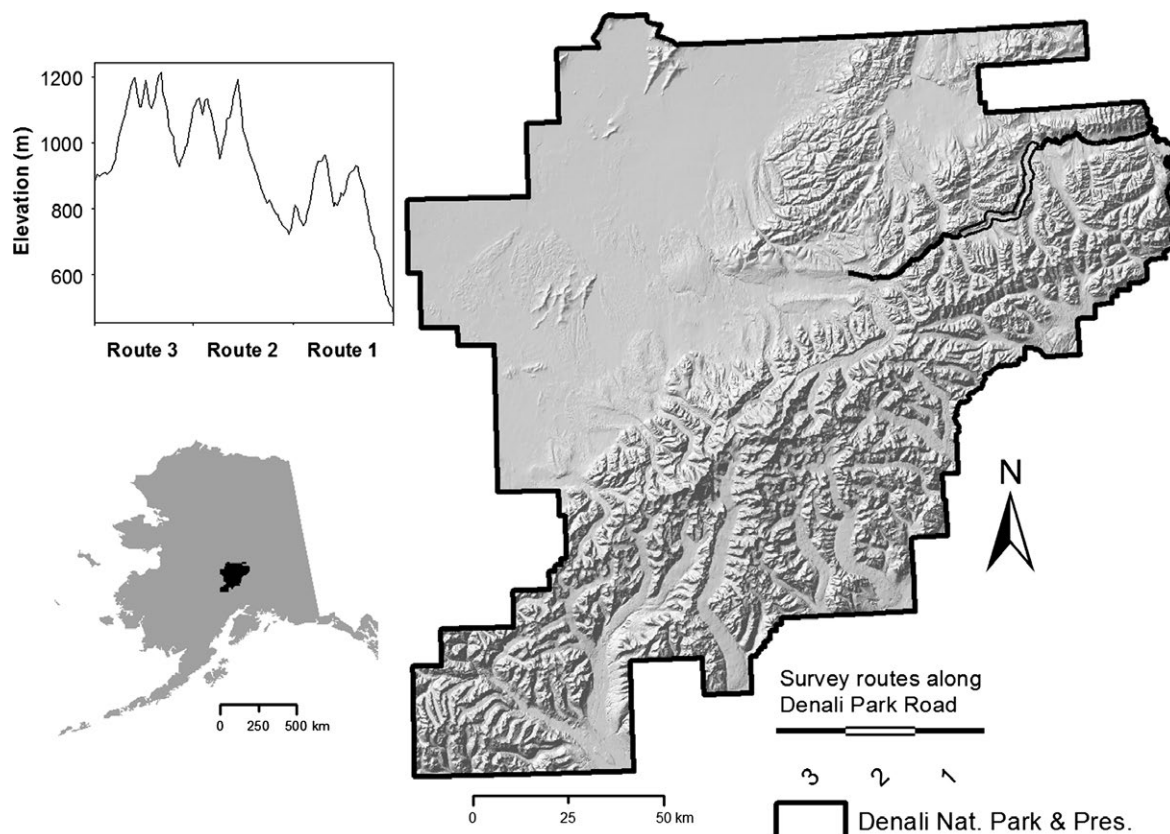
Fig. 1. The location of Denali National Park and Preserve (Denali), Alaska. Survey routes 1–3 along Denali park road are shown in addition to the elevational gradient that they traverse.

some observers conducted surveys in multiple years (Schmidt et al. 2013). We assigned each passerine species to a basic habitat type (Table 1) using the avian-habitat associations from Kessel's (1979, 1998) Alaska avian classification system. Using a 5-m Digital Terrain Model (DTM), average elevation for each point was determined by taking the mean of all raster cells within 200 m (i.e., the area assumed to contain the majority of our detections) resulting in an elevational gradient of 482–1214 m (Fig. 1).

Comparisons of historical and recently repeated photographs (see Appendix A; Roland and Stehn 2014) provided strong visual evidence that changes in vegetation structure have occurred in Denali in recent decades. These changes correspond with significant increases in the mean summer temperature since the 1950s, although temperatures over the shorter term (i.e., during our study) were highly variable (Fig. 2). The gen-

eral trends included increases in vegetative cover and vertical structure, particularly via expansions of woody taxa including erect shrubs into higher elevations, and expansions within ecotonal areas, including the following (see Appendix A):

1. Increasing density and distribution of trees across formerly, relatively open areas with shrub vegetation (Appendix A, Fig. A1–2);
2. Colonization of open, low tundra areas at higher elevations by larger-statured shrubs creating a new, more structurally complex habitat mosaic in these areas (Appendix A, Fig. A3);
3. Widespread conversion of open, gravelly riparian terrace habitats to dense shrub-dominated vegetation cover (Appendix A, Fig. A4).

*Statistical analyses*

We used an occupancy modeling approach (MacKenzie et al. 2006) to detect changes in

Table 1. Parameter estimates and 95% credible intervals for the main and interaction effects of elevation (linear and quadratic) and year on occupancy probability for each of 17 passerine species breeding in Denali National Park and Preserve, Alaska, between 1995 and 2013. Estimates are on the logit-scale and covariates have been standardized to have a mean = 0 and SD = 1. Bold numbers indicate estimates with 95% credible intervals that do not include 0.

| Species | Habitat (Kessel 1979) | Elevation | Elevation$^2$ | Year | Year*elev | Year*elev$^2$ |
|---|---|---|---|---|---|---|
| Fox sparrow | Tall/medium shrub | **0.88** (0.39, 1.40) | **−1.68** (−2.20, −1.23) | 0.39 (−0.29, 1.09) | −0.12 (−0.38, 0.14) | **0.74** (0.44, 1.06) |
| Arctic warbler | Medium/tall shrub | **2.83** (2.03, 3.76) | **−1.32** (−2.22, −0.52) | **−1.32** (−1.93, −0.70) | **−0.67** (−1.10, −0.27) | **1.02** (0.59, 1.50) |
| Savannah sparrow | Low shrub | **1.23** (0.44, 2.02) | −0.54 (−1.22, 0.10) | **−0.68** (−1.17, −0.07) | 0.13 (−0.12, 0.38) | **0.24** (0.01, 0.50) |
| Golden-crowned sparrow | Medium/tall shrub | **3.64** (2.76, 4.67) | −0.10 (−0.89, 0.72) | 0.17 (−0.60, 0.94) | **−1.15** (−1.96, −0.48) | 0.50 (−0.21, 1.17) |
| American tree sparrow | Low/medium shrub | **1.80** (0.94, 2.72) | **−2.05** (−2.96, −1.25) | **−0.74** (−1.47, −0.07) | **0.67** (0.35, 1.02) | 0.08 (−0.29, 0.45) |
| Orange-crowned warbler | Woodland and tall shrub | −0.52 (−1.20, 0.13) | **−1.93** (−2.54, −1.36) | −0.21 (−0.90, 0.52) | **0.57** (0.33, 0.82) | 0.10 (−0.09, 0.29) |
| Wilson's warbler | Tall/medium shrub | 0.53 (−0.04, 1.14) | **−0.76** (−1.17, −0.38) | **−0.93** (−1.83, −0.22) | 0.24 (−0.05, 0.49) | 0.17 (0.00, 0.33) |
| Gray-cheeked thrush | Medium/tall shrub | **−2.64** (−4.47, −1.16) | **−2.83** (−4.53, −1.52) | **0.95** (0.08, 1.93) | **1.37** (0.11, 2.95) | 0.78 (−0.36, 2.24) |
| Dark-eyed junco | Forest and tall shrub | **−5.17** (−6.43, −4.02) | −0.21 (−1.07, 0.75) | **1.39** (0.83, 2.10) | 0.16 (−0.40, 0.83) | 0.01 (−0.54, 0.62) |
| Swainson's thrush | Forest | **−5.19** (−6.91, −3.77) | −0.12 (−1.12, 0.99) | **0.67** (0.14, 1.28) | 0.79 (−0.17, 2.02) | 0.06 (−0.67, 0.87) |
| Yellow-rumped warbler | Forest | **−6.40** (−7.78, −4.93) | 0.03 (−1.06, 1.22) | 1.15 (−0.30, 2.71) | **−0.78** (−1.50, −0.01) | −0.69 (−1.39, 0.03) |
| Ruby-crowned kinglet | Forest | **−4.30** (−5.66, −3.22) | **−1.34** (−1.95, −0.81) | −0.05 (−0.74, 0.74) | −0.47 (−1.08, 0.15) | 0.01 (−0.27, 0.31) |
| Varied thrush | Forest | **−6.20** (−7.78, −4.60) | 0.72 (−0.49, 1.97) | 0.52 (−0.50, 1.83) | 0.26 (−0.78, 1.48) | 0.82 (−0.11, 1.76) |
| Lincoln's sparrow | Wet areas; open forest; medium/low shrub | **−2.06** (−3.04, −1.25) | **−1.33** (−2.00, −0.75) | 0.24 (−0.65, 1.28) | 0.11 (−0.47, 0.74) | −0.04 (−0.44, 0.39) |
| American robin | Forest scrub-generalist | **−3.31** (−4.22, −2.57) | **2.19** (1.35, 3.17) | −0.54 (−1.59, 0.44) | **−0.69** (−1.08, −0.30) | −0.18 (−0.66, 0.27) |
| Hermit thrush | Forest and tall shrub | −0.40 (−1.11, 0.30) | **−0.54** (−1.05, −0.06) | 0.83 (−0.01, 1.65) | **0.53** (0.05, 1.07) | 0.24 (−0.07, 0.61) |
| Blackpoll warbler | Forest and tall shrub | **−2.54** (−4.44, −0.97) | **−2.55** (−4.23, −1.08) | **1.17** (0.04, 2.51) | 0.49 (−0.85, 2.06) | 0.99 (−0.25, 2.50) |

the distribution of each passerine species. We restricted analysis to species detected at >10% of sites in most years to provide sufficient data to adequately model both the detection and occupancy processes. We excluded one ubiquitous species, White-crowned Sparrow (*Zonotrichia leucophrys*), because it was detected at most points in most years leaving little information with which to estimate changes in occupancy rates (i.e., occupancy ≈ 1.0 throughout the study). Our final data set included 17 species (Table 1). Given the discontinuous nature of our dataset, multi-season occupancy models (MacKenzie et al. 2003) were not well-suited for assessing temporal changes in survival and colonization probabilities in relation to elevation. Thus, we used a version of a "single-season" occupancy model (MacKenzie et al. 2002), the "implicit dynamics" model (MacKenzie et al. 2006:186–187), to estimate occupancy ($\psi$) and detection ($p$) probabilities from repeated detection/nondetection data over

multiple years. We fit the occupancy models for each species individually in a Bayesian hierarchical framework using the parameterization and notation of Kéry and Schaub (2012).

In the observation model, $y_{ijt}$ observations were Bernoulli random variables with success probability specified as the product $z_{it}\,p_{ijt}$ in which detection probability $p_{ijt}$ is conditional on the occupancy state $z_{it}$. The $y_{ijt}$ corresponded to detection/nondetection at each point $i = 1, 2, \ldots, I$, during each repeat survey $j = 1, 2, \ldots, J$, in each year $t = 1, 2, \ldots, T$. Based on the results of Schmidt et al. (2013), we specified a model in which $p_{ijt}$ was a linear function of survey date and time after sunrise on the logit-scale:

$$\mathrm{logit}(p_{ijt}) = \beta_0 + \beta_1 \mathrm{date}_{ijt} + \beta_2 \mathrm{date}_{ijt}^2 + \beta_3 \mathrm{time}_{ijt} + \beta_4 \mathrm{time}_{ijt}^2 + e_{\mathrm{obs}(ijt)}$$

We included the linear and quadratic effects of survey timing (relative to sunrise) to account for variation in the probability of availability or diurnal patterns of singing intensity. We included the linear and quadratic effects of survey date to account for variation in the probability of availability over a survey period that typically began prior to the arrival of some individuals and then extended past peak singing (Schmidt et al. 2013). Lastly, we included a random observer effect $e_{\mathrm{obs}(ijt)}$, assuming that observer abilities affect detection (e.g., Link and Sauer 2002).

The occupancy states $z_{it}$ were Bernoulli random variables with parameter $\psi_{it}$. We specified a model in which the logit-transformed occupancy probability $\psi_{it}$ was a linear function of year, elevation (linear and quadratic), two interaction terms, stochastic year effects $\delta_t$, and random site-level adjustments $\alpha_i$ around $\mu$:

we did not utilize model selection procedures. The inclusion of uninformative parameters in species-specific models would lead to conservative conclusions regarding range shifts over time, but erroneously detecting shifts over time was not expected to be an issue. The figures incorporate uncertainty from all parameters and, as such, the credible intervals for the predictions may overlap in some areas despite the "significance" of particular terms.

Inference about changes in distribution was based on the coverage of the credible intervals of the year term and the interaction of year and linear and quadratic elevation, respectively (Table 1). Given inclusion of the interaction terms and scaling of covariate values, the main effects are interpreted as the effect at the average value of the other terms. Thus, the coefficients for the year and interaction terms and the type of distributional change that they indicate depended on where a species' elevational distribution lay in relation to the mean elevation of our sample. Although inference about the presence of distributional change was based on the coverage of the credible intervals for these three terms, we also produced graphical predictions based on average covariate values to help visualize the type of distributional change (e.g., an overall decrease or increase in occupancy, a range shift, or range expansion) which was not term specific.

We fit models using WinBugs 1.4.3 (Spiegelhalter et al. 2004) via the R2WinBUGS package (Sturtz et al. 2005) in program R 3.0.2 (R Core Development Team 2013). We used diffuse pri-

$$\mathrm{logit}(\psi_{it}) = \mu + \alpha_i + \alpha_1 \mathrm{year}_t + \alpha_2 \mathrm{elev}_i + \alpha_3 \mathrm{elev}_i^2 + \alpha_4 \mathrm{year}_t \times \mathrm{elev}_i + \alpha_5 \mathrm{year}_t \times \mathrm{elev}_i^2 + \delta_t$$

Based on the theoretical shift patterns of range dynamics identified by Breshears et al. (2008) and Maggini et al. (2011), we included terms for the interaction of year with both the linear and quadratic effect of elevation to allow response curves to both shift and change shape. This full model was then fit to the data from each individual species. While fitting a single model for each species may not result in the most parsimonious model possible, for the purposes of this study,

ors on all parameters (i.e., uniform distributions from 0 to 100 for the standard deviations of the random effects; uniform distributions for all fixed occupancy and detection covariates with the exception of survey timing effects and year term which had normal distributions with mean 0 and precision 0.01). Summaries of the posterior distribution were calculated from three independent Markov chains run for 12 000 iterations with a 4000 iteration burn-in and thinning every two
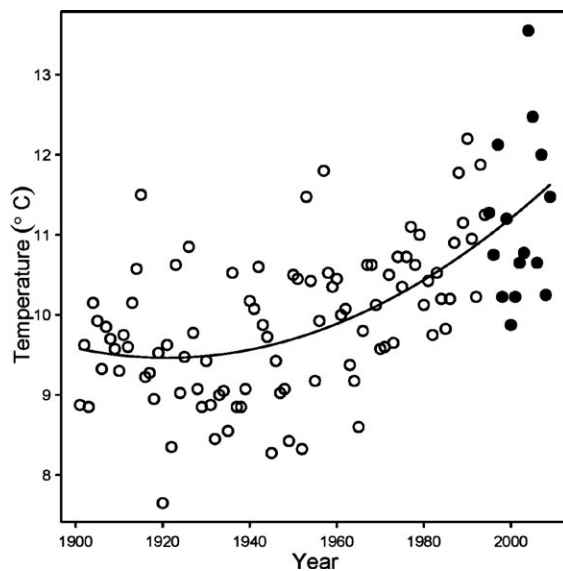
Fig. 2. Trend in the estimated mean monthly summer (May–August) temperatures (degrees C) for one subalpine SNAP (Scenarios Network for Alaska and Arctic Planning 2014) grid cell within in our study area. There was a significant increasing curvilinear trend in mean summer temperature from 1901 to 2009 (adjusted $R^2$ = 0.3974, $P$-value <0.00001). Filled circles correspond to temperatures occurring during the period of overlap (1995–2009) between our study and SNAP data coverage within which there was not a significant linear trend in summer temperature (adjusted $R^2$ = −0.04, $P$-value = 0.53).

draws. We assessed convergence visually and using the Gelman-Rubin diagnostic (Brooks and Gelman 1998) and scaled continuous covariates (mean = 0, SD = 1) to improve convergence properties. All estimates are presented as posterior means with 95% Bayesian credible intervals.

## RESULTS

Most of the passerine species that we considered shifted or expanded their distribution in the predicted direction based on individual habitat associations (Figs. 3–4). All species associated with shrub habitats exhibited changes in distribution (Table 1), the majority of which were upward shifts in the core of their elevational distributions (Fig. 3b–f). Relative to their elevational breadth, the largest distributional changes were exhibited by Arctic Warbler

(*Phylloscopus Borealis*), Savannah Sparrow (*Passerculus sandwichensis*), and Golden-crowned Sparrow (*Zonotrichia atricapilla*) (Fig. 3b–d). The shifts in optimum elevation exhibited by Arctic Warbler and Savannah Sparrow were the largest that we observed and also resulted in a portion of the population occupying elevations outside our sampling frame (at higher elevations).

Among the remaining shrub-tundra species, American Tree Sparrow (*Spizella arborea*) and Orange-crowned Warbler (*Oreothlypis celata*) exhibited upward shifts (Fig. 3e–f). Fox Sparrow (*Passerella iliaca*) showed range expansion at both low and high elevations (Fig. 3a). Wilson's Warbler (*Wilsonia pusilla*) appeared to show a declining temporal trend in occupancy across its elevational range, although there was some uncertainty as to whether it was shifting upwards as well (Fig. 3g; Table 1). Dark-eyed Junco (*Junco hyemalis*), Yellow-rumped Warbler (*Setophaga coronata coronate*), and Swainson's Thrush (*Catharus ustulatus*), forest-associated species, showed leading edge range expansions (Fig. 4a–c; Table 1). The distribution of American Robin (*Turdus migratorius*) retracted along its leading edge (Fig. 4g), whereas Ruby-crowned Kinglet (*Regulus calendula*) and Varied Thrush (*Ixoreus naevius*) showed limited evidence of changes in distribution over time (Table 1; Fig. 4d–e).

We also observed colonization of our study area by one shrub-tundra species and two forest-tall shrub species, Gray-cheeked Thrush (*Catharus minimus*), Hermit Thrush (*Catharus guttatus*), and Blackpoll Warbler (*Setophaga striata*), respectively. These species were nearly absent during the initial years of our study but colonized sites located across the elevational gradient with distributional peaks at mid-elevations around treeline (Figs. 3h and 4h–i). The lone wetland species that we considered, Lincoln's Sparrow (*Melospiza lincolnii*), showed limited evidence of changes in distribution over time (Table 1; Fig. 4f).

## DISCUSSION

Our results demonstrated temporal change in the passerine community along the DPR over an elevational gradient, with most species (i.e., 14 out of 17; Table 1) exhibiting directional changes in distribution and/or occupancy during
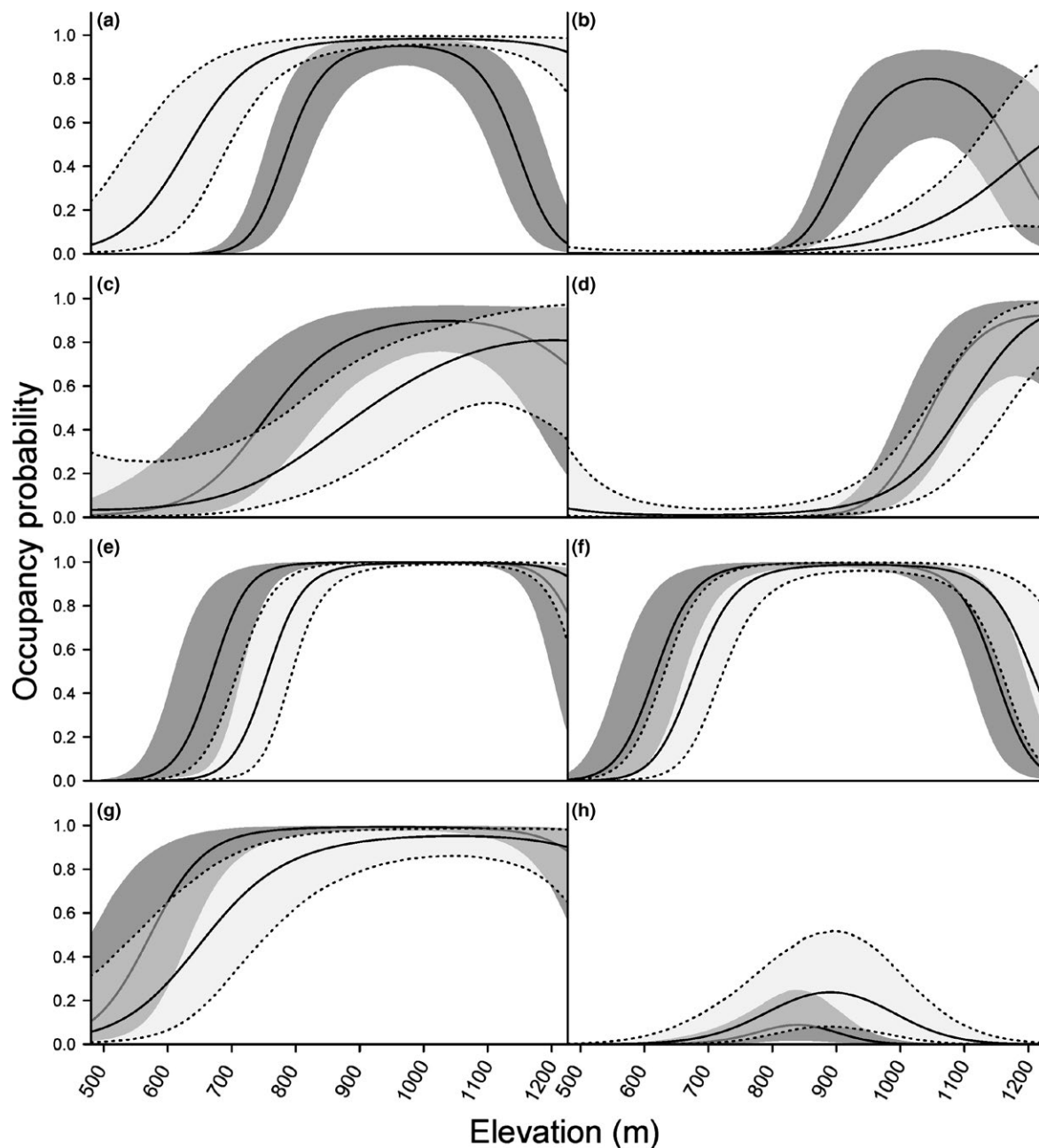
Fig. 3.   Predictions of occupancy probability in relation to elevation for shrub-tundra passerines in year one (1995) and year 19 (2013) of our study in Denali National Park and Preserve, Alaska. Posterior means for both years are solid lines. For 1995, 95% credible intervals have a gray fill. For 2013, 95% credible intervals are dashed with a transparent fill. Species include (a) Fox Sparrow, (b) Arctic Warbler, (c) Savannah Sparrow, (d) Golden-crowned Sparrow, (e) American Tree Sparrow, (f) Orange-crowned Warbler, (g) Wilson's warbler, and (h) Gray-cheeked Thrush.

our 19-year study. These changes were consistent with species-specific habitat associations and observed long-term changes in the structure and distribution of vegetation communities in the study area (Stueve et al. 2011, Roland and Stehn 2014). All shrub-tundra species showed
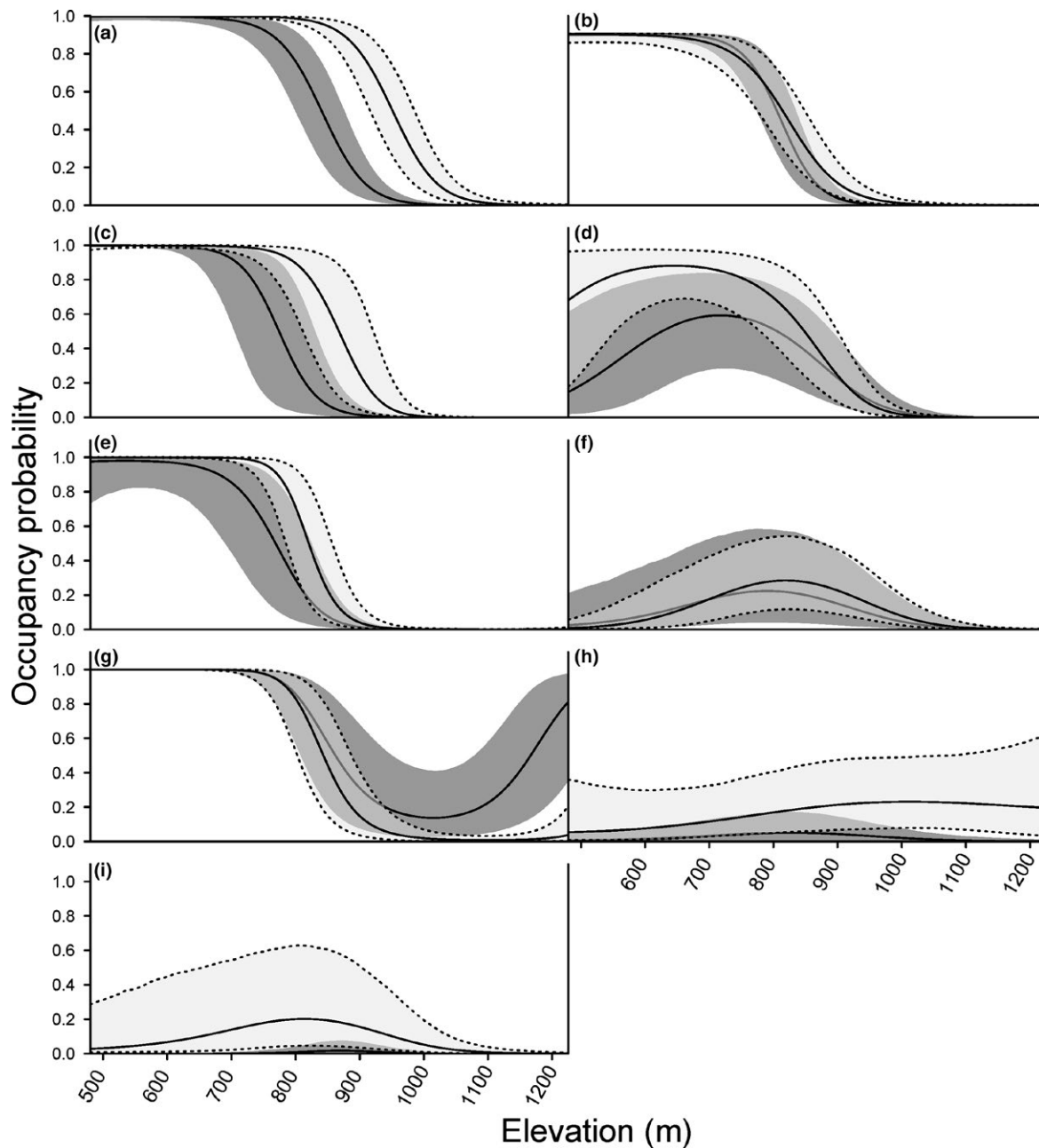
Fig. 4. Predictions of occupancy probability in relation to elevation for forest passerines and one wetland passerine (Lincoln's Sparrow) in year one (1995) and year 19 (2013) of our study in Denali National Park and Preserve, Alaska. Posterior means for both years are solid lines. For 1995, 95% credible intervals have a gray fill. For 2013, 95% credible intervals are dashed with a transparent fill. Species include (a) Dark-eyed Junco, (b) Swainson's Thrush, (c) Yellow-rumped Warbler, (d) Ruby-crowned Kinglet, (e) Varied Thrush, (f) Lincoln's Sparrow, (g) American Robin, (h) Hermit Thrush, and (i) Blackpoll Warbler.

changes in distribution, and the majority exhibited an upward shift in the core of their elevational distributions, consistent with previous work showing increased shrub cover at higher elevations in the subarctic over time (Dial et al. 2007, Hallinger et al. 2010,

Myers-Smith 2011). Forest-associated passerines showed a weaker response as a group with several species showing unexpected responses (i.e., range stability or retraction) and others exhibiting modest leading edge expansions, consistent with slower advancement of the treeline ecotone in Denali (Stueve et al. 2011).

Although we did not have direct measures of vegetation change for inclusion in our analysis, the patterns and magnitude of elevational range shifts closely matched our predictions based on broadly documented vegetation changes and species-specific habitat associations, suggesting that changes in bird distribution were ultimately related to vegetation change. Denali's mean summer temperature (May–August) has increased significantly over the past century, but remained stable over our 19-year study period (Fig. 2), further suggesting that climate may indirectly affect bird distribution through long-term changes in vegetation. That is, the distributional responses that we observed (coupled with little evidence of a change in mean temperature over the study period) suggests that passerines may respond rapidly to changes in woody vegetation once suitable structure is established, but the latter process is occurring over comparatively longer timescales largely via the direct effects of abiotic factors. This is consistent with other work demonstrating that species distribution models that do not account for time lags in the response of woody vegetation may predict highly biased estimates of bird species richness (Kissling et al. 2010).

As predicted, we found the largest distributional changes in species associated with the shrubline ecotone. Arctic Warbler, Savannah Sparrow, and Golden-crowned Sparrow exhibited some of the largest shifts (relative to their elevational breadth) and occupancy declines of the species we considered. Savannah Sparrow is associated with open, low shrub habitats (Kessel 1979, 1998), and Golden-crowned Sparrow is an alpine, shrub thicket specialist in Denali (Kessel 1989). Arctic Warbler is found in higher densities in willow (*Salix* spp.) dominated, open shrub habitats (Hagelin et al. 2010) and has morphological adaptations for using fluttering forage tactics to capture aerial insects from open shrub crowns (Batova 2011). We expected these species to be the most sensitive to shrub infilling and

encroachment due to their shrubline association and, in the case of the latter two, their relatively compressed elevational ranges. While the distributions of these species could have shifted to elevations outside our sampling frame, vegetation studies in Denali found that mean shrub cover in the >200-cm height class is <1% above 1200 m (C. Roland, unpublished data). In addition, shrub colonization at these elevations is limited to a large extent by topographic and edaphic characteristics, i.e., steep, disturbed slopes, and barren rock outcrops which cover approximately a third of Denali. Thus, for medium-tall shrub-tundra species like Arctic Warbler and Golden-crowned Sparrow, occupancy might increase at higher elevations, but there is limited capacity in the near future for expansion of upper range margins beyond the elevational gradient in our sampling frame. Limited potential habitat above 1200 m and current estimates of population trends suggest that these species may be most at risk in our study area under continued warming.

Other shrub-tundra species, including Orange-crowned Warbler and American Tree Sparrow, were more widely distributed and achieved maximum occupancy over much of the elevational gradient (Fig. 4b–c). Orange-crowned Warbler is widely distributed across western and northern North America and nests in a variety of woodland and shrub habitats (Gilbert et al. 2010). American Tree Sparrow is associated with low and medium shrub habitats usually near treeline (Kessel 1979, 1998, Naugler 1993). Therefore, both species use habitats that are expanding upwards in the subarctic (Dial et al. 2007, Hallinger et al. 2010, Myers-Smith 2011). Upward shifts in the lower range margins of these species (Fig. 3e–f) may have been due to forest infilling (e.g., Stueve et al. 2011) and/or changes in shrub stature and cover within small areas of low elevation woodland where these species were initially found in low abundance.

Fox Sparrow was unique in that its elevational range expanded along both leading and trailing edges, leading to an overall increase in occupancy. In contrast, the probability of occupancy for Wilson's Warbler decreased through time throughout its range. These trends in occupancy are consistent with the findings of Schmidt et al. (2013), who found a 250% increase in Fox Sparrow abundance and a 48% decrease in Wil-

son's Warbler abundance in the study area from 1995 to 2009. Our results suggest that elevational range expansion underlies the observed trend in Fox Sparrow abundance, whereas Wilson's Warbler abundance was likely declining across the elevational gradient.

Changes in the distributions of forest-associated species primarily occurred in the 800- to 1000-m elevation zone. This finding is consistent with a study of treeline dynamics in Denali from 1953 to 2005, which found that tree establishment rates were highest in the 800- to 1000-m elevation zone and considerable infilling occurred at lower elevations (Stueve et al. 2011). In addition, the upper tree limit (of trees of any height or density) advanced approximately 150 m in elevation on south-facing slopes, the dominant exposure of the park road corridor (Stueve et al. 2011). Given this rate of upslope migration and the relatively sparse distribution and short stature of trees near the upper tree limit, it would not be surprising if changes in the distribution of some forest passerines, particularly species requiring mature tree cover, were occurring over longer timescales compared with shrub-tundra passerines. The structure and composition of forest below the treeline ecotone would be expected to change little at the decadal scale, absent large-scale disturbance such as fire. This corresponds with a weaker response of forest-associated species as a group, particularly those species requiring mature tree cover (e.g., Varied Thrush).

Lincoln's Sparrow, a species associated with poorly drained, boggy areas and a wide range of vegetation structural characteristics (Kessel 1979, 1998, Ammon 1995), was one of the few mid-elevation species showing little change in either distribution or occupancy. Although the distribution of boggy areas may change, one would expect that a warming and drying climate would not drive upslope shifts in the distribution of these habitats. Poorly drained sites at high elevations are topographically constrained and thus are already quite limited in their distribution by generally steep slopes in subalpine to alpine areas. A lack of response by Lincoln's Sparrow may suggest that they are not selecting breeding areas based primarily on vertical structure (i.e., shrub and tree cover) and that distributional change in boggy habitats (e.g., greater fragmentation) may be occurring over timescales longer

than the duration of our study. Thus, heterogeneity in passerine responses to climate change could arise because the distributional responses of some vegetation communities (e.g., wetland-associated) may not be directional (e.g., fragmentation vs. an upslope shift), or they could differ from the overall pattern of directional change on the landscape.

The potential for nondirectional changes in vegetation distribution illustrates the importance of considering both changes in passerine distribution and population size, as sometimes only the latter might change when shifts in vegetation distribution are nondirectional. Floodplain ecotones may provide an additional example. At low elevations, floodplain ecotones bisect upland forest and treeline, but shrub colonization in these areas represents potential habitat for shrub nesters with distributions centered above treeline. Therefore, unexpected responses among shrub-tundra species (e.g., downslope expansion by Fox Sparrow) could potentially arise due to shrub expansion on floodplain ecotones at low elevations.

Reorganization of species assemblages via distributional change alters the competitive environment and can lead to shift patterns that run counter to expectations including downslope shifts (Lenoir et al. 2010). Although species declines and/or shifts in distribution within the established community may alter competitive interactions, invading species may also dramatically affect species dynamics and community structure (Gilman et al. 2010, Lenoir et al. 2010). Blackpoll Warbler, Hermit Thrush, and Gray-cheeked Thrush were colonizers in our study area. American Robin exhibited a leading edge retraction that could have been due to competitive interactions with the two invading congener thrush species (Hermit and Gray-cheeked Thrush), but many other mechanisms are also possible. Although additional research is needed to quantify changes in distribution due to competitive interactions, the changes in community composition that we observed indicate that competition could be an important factor in determining future patterns of distribution.

Our study suggests that passerines associated with shrub communities in the northeastern region of Denali are shifting upwards, possibly in concert with vegetation change. Although we de-

tected a weaker signal from forest-associated species as a group, consistent with a slower rate of tree recruitment, several of these species showed range expansion near treeline. This occurred amidst colonization (primarily near treeline) by three species that were nearly absent at the beginning of our study. Thus, rapid alteration of the passerine community in our study area is occurring through the convergence of strong distributional change across multiple geographic dimensions. This type of change may trigger complex and potentially transitory changes in species interactions and community structure and thus presents challenges for accurate prediction of the community trajectory into the future (Suttle et al. 2007, Gilman et al. 2010).

Despite theoretical predictions of poleward and upslope responses of passerines to climate change, empirical studies have often reported variable responses with some species shifting opposite of the expected direction and others showing no change in distribution (Archaux 2004, Popy et al. 2010, Tingley et al. 2012). Our results suggest that this heterogeneity may be partially explained by the ecological relationships between individual species and changing vegetation communities, rather than responses to increases in mean temperature alone. The elevational distributions of many passerines in our study area correspond to the distribution of distinct and relatively simple vegetation structures and ecotones, and when the ecology of each species is considered, the pattern of these responses provides a broader context for landscape change in Denali. The implications for avian conservation and long-term monitoring are profound. Distributional shifts of passerine species may complicate the understanding of apparent population declines particularly when sampling frames are truncated relative to species' distributions along elevational gradients. That is, estimating trends in occupancy or abundance without assessment of change over time relative to elevational or vegetation gradients could lead to ambiguous interpretation as these trends could mimic distributional shifts. This highlights the importance of considering ecological relationships when assessing the effects of climate change on passerine populations and communities. To more fully understand the long-term implications of continued climate warming, it will likely be necessary to quantify the direct effects of climate on habitats in addition to basic monitoring of population trends.

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